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Notes on the Development of a Trap-door Spider, *Ummidia fragaria* (DOENITZ)

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The development of spiders is distinctly divided into three periods : an embryonal, a larval, and a nympho-imaginal stage. According to HOLM (1940, 1954) and VACHON (1957, 1958) the type of development in the larval stage varies greatly in the different groups. Therefore it may be significant to investigate the morphogenesis during the larval period from a point of view of phylogeny. The author studied the development of *Heptathela kimurai* (Heptatheridae) (1954—55) and *Atypus karschi* (Atypidae) (1958). In order to compare the developmental type of the larvae of these spiders with that of *Ummidia fragaria* (Ctenizidae) this investigation has been carried out.

Ummidia fragaria is common in Kyushu. Their breeding season ranges from the middle of July to the beginning of August. The nests are found on tree trunks or stone walls. They are fingerstall-like in form, about 30—35mm in length, and have a hinged door. The door is a thin, wafer-like structure, roughly oval in outline, and measures about 12 × 13 mm in width. The outer surface of the nest is covered with moss. The egg sac is suspended from the wall of the nest by a few threads. It is almost pentagonal or polygonal in shape, about 12—15 mm in diameter, about 5—7mm in thick. The egg mass is ellipsoidal in shape, about 5—8 mm in diameter, about 3—4 mm in thick, and consists of nearly 60 eggs. The eggs are light orange, almost spherical, about 1—1.2 mm in diameter, and are surrounded by a chorion. To make the chorion more transparent and to observe the embryos in detail, the eggs were put in paraffin oil. The eggs hatch in 21—22 days (24—30°C).

Embryonic Development

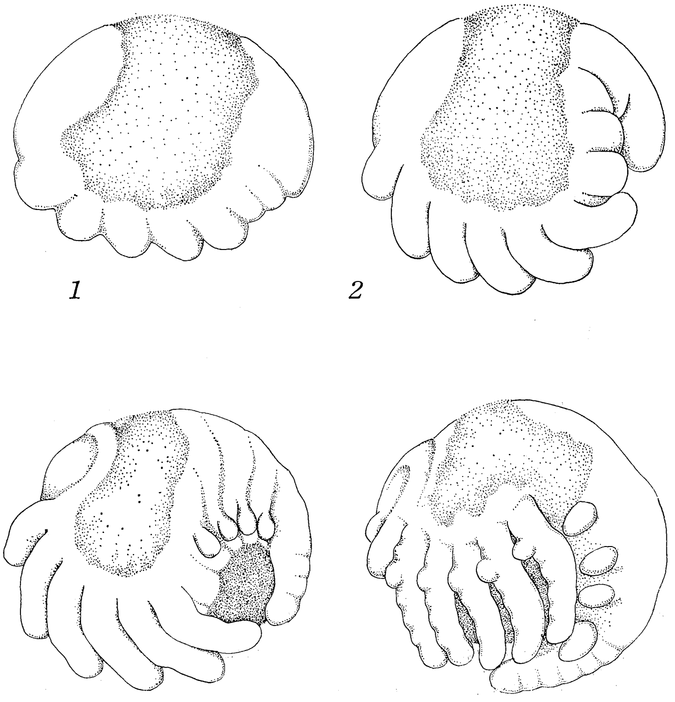
About four days after oviposition the cleavage nuclei reach the egg periphery, the periplasm, where they form a single cell layer, the blastoderm. At this time the blastoderm cells number about 60—70 ; they are larger, polygonal in shape, about 200—250μ in diameter, and equally distributed over the egg surface. As cleavage proceeds, they become smaller and rounded, eventually measuring about 30μ in diameter. When the number of blastoderm cells has attained to about 200—300, the contraction of the blastula occurs. At this time a clear fluid emerges from the inside of the blastula ; this fills up the upper part of the egg ; thus the perivitelline cavity is formed.

About eight days after oviposition small white flecks appear on the surface of the blastula. Of these the fleck located in the center of the flat upper (ventral) side of the embryo becomes gradually wide to form the primitive plate. Then a small elevation, the primitive cumulus, appears in the plate. It migrates from the primitive plate to the edge of the flat upper side of the embryo, where it becomes flatter and flatter and ultimately disappears. The primitive plate, after separation of the primitive cumulus, becomes the germ disk or ventral plate.

About eleven days after oviposition the metamerization of the germ disk occurs. At first five transverse grooves appear on the germ disk. As a result of this segmentation four leg segments are formed between the indefinite cephalic lobe and the caudal lobe. Then the indefinite cephalic lobe is divided into the cephalic lobe, the cheliceral segment, and the pedipalpal segment. On the other hand, the caudal lobe cuts out successively the abdominal segments forward (Fig. 1). Thus the germ disk extends and changes into a segmented germ band. Meanwhile the rudiments of the cephalothoracic appendages appear. Except the cephalic lobe and the caudal lobe every segment of the germ band becomes divided into right and left halves by the ventral sulcus. As development proceeds, the halves of the germ band become more widely separated.

In this stage the cephalic lobe is semicircular and somewhat elevated (Fig. 5). Just behind the lobe lies the cheliceral segment, on which the rudiments of the chelicerae are developed. The rudiments of the pedipalps and legs are prominent and nipple-like in form. In the abdominal portion there are three or four segments and the caudal lobe.

After the fourth abdominal segment has been cut out from the caudal lobe, the caudal lobe elevates, bends forward (Fig. 2), and cuts out successively the posterior abdominal segments. Such a developmental pattern of the abdominal portion is designated as the Haplogynae-type (HOLM, 1940, 1954). The cephalic lobe is somewhat elevated and is divided into right and left halves by the an-



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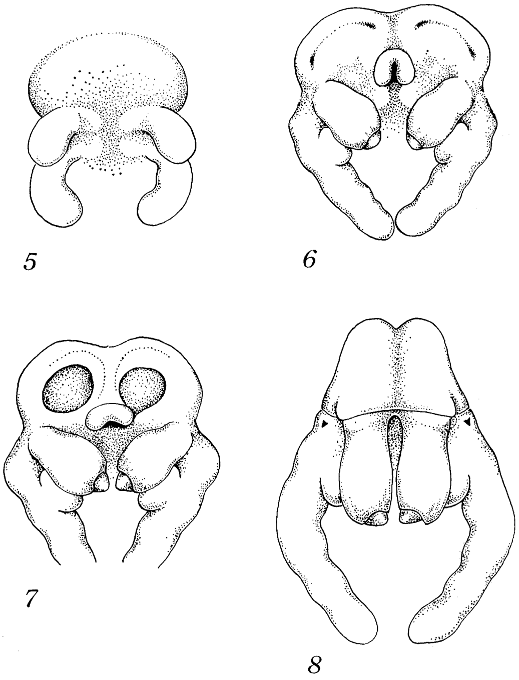
3 4

Figs. 1—4. Embryos of *Ummidia fragaria*

1. Embryo of about 11 days ; the cheliceral segment is not yet separated from the cephalic lobe, other prosomal segments are separated ; 2. Embryo of about 13 days ; the caudal lobe is lifting ; the prosomal appendages are developed ; 3. Embryo of about 15 days ; the abdominal appendages appeared ; 4. Embryo of about 16 days ; the postabdomen pushes between the prosomal appendages ; the brain formation begins.

terior sulcus. After the caudal lobe has cut out the seventh abdominal segment, the stomodeal pit appears in the cephalic lobe ; it is surrounded with the horseshoe-shaped rostrum. The chelicerae are nipple-like in form. The pedipalps and legs are finger-like in form and all of them have a marked tumescence, the sterno-coxal process, on the antero-mesial side of their coxal portion. After the caudal lobe has cut out the eighth abdominal segment, four



Figs. 5—8. Changes in the cephalic lobe of *Ummidia*.

5. Embryo of about 12 days ; 6. Embryo of about 16 days ; the rostrum and the sterno-coxal processes are well developed ; 7. Embryo of about 18 days ; the brain formation is proceeding ; 8. Embryo of about 21 days ; the egg-teeth appeared.

pairs of appendage primordia appear on the second to fifth abdominal segments (Fig. 3).

About fifteen days after oviposition the cerebral grooves appear in the antero-lateral marginal region of each half of the cephalic lobe (Fig. 6). The rostrum is well-developed and the stomodeum deepens. The chelicera has been segmented into two ; and the terminal segment is small and rounded. The pedipalps and legs are considerably elongated and their sterno-coxal processes are well-developed (Fig. 4). The abdominal portion extends to an antero-ventral direction ; and it is composed of ten segments and the telson. Seen laterally the embryo at this stage shows that each half of the germ band is strongly curved in the form of an S, the cephalothoracal portion convex ventrally, then the abdominal portion convex dorsally. The two halves of the germ band move further in a latero-dorsal direction and the dorsal borders of the posterior abdomen fuse in the dorsal median line. Subsequently the segments ahead successively are closed dorsally in the same way.

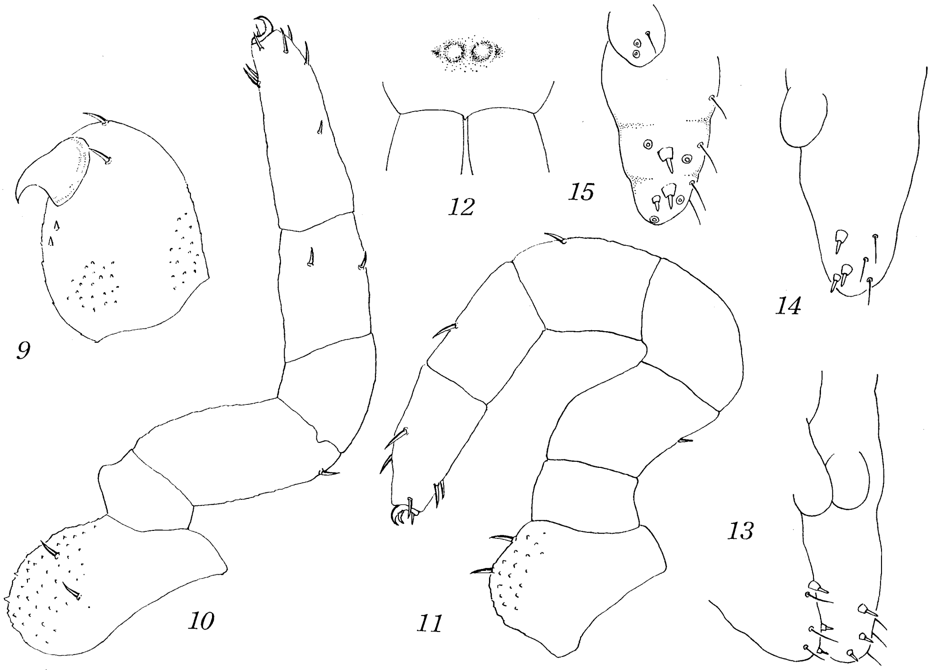
About seventeen days after oviposition the brain formation begins. On the antero-lateral edge of each half of the cephalic lobe the cephalic fold arises. Both the cephalic folds fuse together and this covers the cerebral grooves and then the whole surface of the cephalic lobe (Fig. 7). Thus the brain formation proceeds. On the dorsal side of the cephalothoracal portion the carapace is formed. The chelicerae located on either side of the mouth move forward and mesad and nearly meet in front of the rostrum. The rostrum changes to the labrum. The basal segment of the chelicera is robust ; and the fang rudiment is conical in shape. The pedipalps and legs are more remarkably elongated than the chelicerae. At the end of this stage the egg-tooth is formed on the base of each pedipalp as a thick cuticular structure (Fig. 8).

As a result of yolk removing from the cephalothorax to the abdomen the abdominal portion becomes remarkably bulged. All the abdominal segments are closed in the mid-dorsal line, where the heart is completed. The first abdominal segment becomes gradually narrower, transforming into the pedicel. The first and second abdominal appendages become flattened, eventually transforming into the lung plates, which have a small invagination on their postero-lateral side. Later these invaginations will become the lung sacs. The third abdominal appendages are missing. The fourth abdominal appendages are the common rudiments of the middle and hind spinnerets ; and the bifurcation of them is distinctly recognized. The last segment, the telson, becomes the anal tubercle, where the proctodeal invagination is formed.

Postembryonic Development

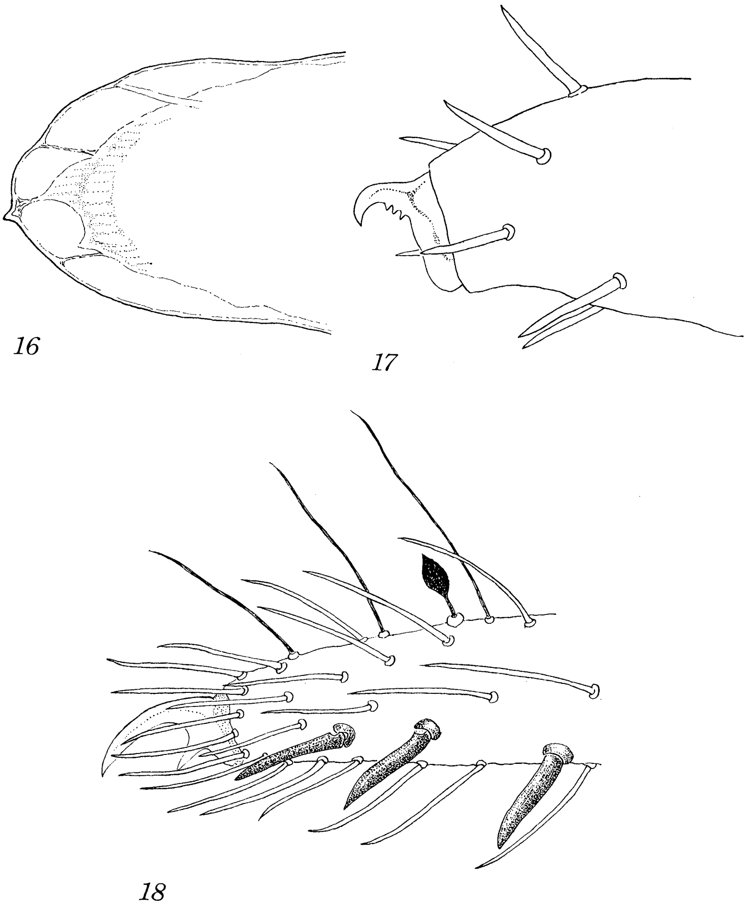
Prelarva — The newly hatched spiderlings, the prelarvae, are almost immobile, about 1. 6 mm long, milky white in color, but the light orange or yellow yolk is seen through the cuticle. At the time of hatching the egg-teeth drop off. The carapace is almost round and somewhat elevated. Eyes are not yet formed. The chelicerae project forward. The fang rudiment is conical, and pointed at the tip. The pedipalps are leg-like in form ; their segmentation is distinct. They have no setae and claw. However the tip of the pedipalp has a small projection (Fig. 16). The sterno-coxal processes are still recognized. The legs are similar in appearance to the pedipalp, but the sterno-coxal processes are completely reduced. The tip of the leg has a small projection. There are no setae and claws. The rostrum was transformed into the labrum. The sternum is an elevated shield-like plate, on its fore edge the labium will be formed later. The pedicel is thick and contains yolk. The abdomen is globose and ten segments are visible. On the ventral side of the second and third abdominal segments there are two pairs of book lungs. On the ventral side of the fifth abdominal segment there are two pairs of spinnerets. The middle spinnerets are smaller and have no spinning tubes ; the hind spinnerets are larger and have three spinning tubes (Fig. 13). About two days after hatching the first molt occurs.

Larva — Through the first molt the prelarva becomes the larva, which is about 2 mm long, milky white in color, and walks about slowly. The carapace is nearly round and somewhat elevated. A deep transverse thoracic groove is



Figs. 9—11. Prosomal appendages of *Ummidia* larva
9. Right chelicera ; 10. Right pedipalp ; 11. Right walking leg I.
Fig. 12. Eye region of *Ummidia* larva
Figs. 13—15. Stages in the development of middle and hind spinnerets of *Ummidia*
13. Prelarval stage ; 14. Larval stage ; 15. Protonymphal stage.

visible. Two or three days after molting the eye area becomes pigmented with blackish brown (Fig. 12). The basal segment of the chelicera is robust and has several short setae and two small cheliceral teeth (Fig. 9). The fang segment is conical, but has a short sharply curved tip. It is tinged with light brown. The pedipalp has a few short setae and a toothed claw (Fig. 17). There is no sterno-coxal process (Fig. 10). The leg has a few short setae and two toothed claws (Fig. 11). The median claw rudiment is not recognized. The sternum is



Figs. 16—18. Stages in the development of the pedipalpal tarsus of *Ummidia*

16. Prelarval stage ; tendons of levator and depressor muscles are visible ; 17. Larval stage ; 18. Protonymphal stage ; there are a club-shaped seta and three long sensory hairs on the dorsal side and two rows of three or four strong spines on the ventral side.

round or oval, quite smooth, and slightly elevated in the middle. The labium is separated from the sternum by a transverse groove.

The abdomen is oval and its segmentation is distinctly recognized. There are no setae on the dorsum ; two pairs of muscle impressions are visible. The ventral side of the abdomen is clothed with scattered short setae. The lung plates are somewhat elevated. The spinnerets are situated near the anal tubercle. The middle spinneret is smaller and consists of one segment. It has no spinning tube. The hind spinneret is larger, about four times as long as the middle spinneret, and consists of three segments (Fig. 14). The middle segment has one and the distal segment has two spinning tubes. The anal tubercle is somewhat protruded.

Protonymph — The larval stage continues about four weeks. After the second molt the larvae become the protonymphs ; they are active and spin the draglines. They remain within the egg sac and enter into the hibernation.

The protonymph is about 2 mm long, but resembles the adult in form except size and secondary sexual characters. The carapace is nearly oval and brown in color. The pars cephalica is somewhat elevated and has a few setae. The eye region is slightly convex and deeply pigmented with blackish brown. Eight eyes are distinctly recognized. The pars thoracica is smooth and has a procurved fovea and shallow radial furrows. The chelicerae are directed forward and obliquely downward. They are robust, bluish black, and have a rake rudiment in front. The outer margin of the chelicera has four larger teeth and the inner four smaller teeth. The fang is brown and claw-like in shape. The pedipalps and legs are light yellow, with bluish black annulations, and armed with strong spines (Table 1). The pedipalp has no maxillary lobe. The tarsus has a toothed claw, about three long sensory hairs, and a club-shaped seta (Fig. 18). The legs have many sensory hairs, but in the fourth legs they are few. In this stage the legs, unlike the adult, have no club-shaped setae. The tarsus bears

Table 1. Number of spines of *Ummidia* protonymph

	Coxa	Trochanter	Femur	Patella	Tibia	Metatarsus	Tarsus
Pedipalp	6	0	1	1	6		6—7
Leg I	0	0	0	0	3—4	6	3—4
II	0	0	0	0	1—2	4	3
III	0	0	0	1	0	2	0
IV	0	0	0	0	0	0	0

three claws ; the upper claws have several comb teeth, but the lower claw is simple. The sternum is round, light yellow, and clothed with some short hairs. The labium is trapezoid and bears two or three spines.

The abdomen is nearly spherical. The dorsum is brown violet with light yellow spots. The segmentation is still recognized especially in the postabdomen ; and each segment has short hairs. The ventral side of the abdomen is light brown violet, but the lung plates are pale. The middle spinneret is simple and has two spinning tubes (Fig. 15). The hind spinneret is longer with four segments. The basal segment has no spinning tube. The second has 0—1, the third has 3, and the terminal segment has 4—6 spinning tubes.

Discussion

When we compare the embryonic development of *Ummidia* to that of *Heptathela* or of *Atypus*, we find that the embryonic development of *Ummidia* is very similar to that of *Atypus*, but differs very markedly from that of *Heptathela*. The main characteristics of the embryonic development of *Heptathela* are as follows. 1. In *Heptathela* the primitive cumulus does not appear in the primitive plate, whereas in *Ummidia* and *Atypus* it is distinctly recognized. 2. The ventral sulcus never widens throughout the embryonic development. 3. The sterno-coxal process does not appear in each of the pedipalps and legs. The development of the sterno-coxal process seems to be peculiar to the mygalomorphs. 4. The widening of the ventral sulcus does not occur ; the developmental pattern of the abdominal portion is the Haplogynae-type ; so that the process of reversion can be scarcely recognized. 5. In *Heptathela* the appendages of the fourth abdominal segment are divided into the exopodite and the endopodite, whereas in *Atypus* they are unbranched and in *Ummidia* they are completely reduced.

On the other hand, the embryonic development of the mygalomorphs is very similar to that of the haplogyne spiders.

A comparison of different types of larval development of spiders may be significant for phylogeny. In *Heptathela* and *Atypus* the spiderlings just after hatching are the larvae (L), whereas in *Ummidia* they are the prelarvae (pL). Two days after hatching they take the first molt and become the larvae ; so that the larval stage of *Ummidia* consists of two phases : pL, L. In *Ischnothele* (Dipluridae) also the larval stage consists of pL, L (Holm, 1954), whereas in

Grammostola (Theraphosidae) L, pN (VACHON, 1958). Jezequel (1961) studied the postembryology of a theraphosid spider and stated that the larval stage of this spider consists of only one phase, L. But his "première nymphe" is considered to be the prenymph (pN) in organization. The larval stage of *Heptathela* is simple, L ; about three days after hatching the first molt occurs and the larvae transform into the complete protonymphs ; so that this type is the most primitive. In *Atypus*, about ten days after hatching the larvae become the protonymphs. However, they are still unpigmented except the eye region. This stage lasts about three weeks and after the second molt they become the deutonymphs, which are brown in color. The larval stage of Dipluridae, Ctenizidae, and Theraphosidae consists of two phases. Therefore it may be concluded that the Atypidae is the most primitive among the mygalomorphs from the point of view of comparative embryology.

Summary

1. The embryonic and the early post-embryonic development of *Ummidia fragaria* (Ctenizidae) was studied on preserved and living materials.

2. The embryonic development of *Ummidia* closely resembles that of other mygalomorphs.

3. In about three weeks the eggs hatch and the prelarvae emerge. About two days after hatching they take the first molt and become the larvae. The larval stage lasts about four weeks and the larvae transform into the protonymphs. The early postembryonic development of *Ummidia* is very similar to that of *Ischnothele* (Dipluridae).

4. In Ctenizidae, Dipluridae and Theraphosidae the larval stage consists of two phases : pL, L or L, pN, whereas in Atypidae only one phase, L. In the primitive spider, *Heptathela* also the larval stage is only one phase, L. From a point of view of comparative embryology, therefore, the Atypidae may be the most primitive among the mygalomorph spiders.

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Note added in proof : Since writing this, COYLE has published a paper, "Systematics and natural history of the mygalomorph spider genus *Antrodiaetus* and related genera (Araneae : Antrodiaetidae). Bull. Mus. Comp. Zool., 141 : 269-402 (1971). The pattern of early postembryonic development of *Antrodiaetus* is similar to that of *Ummidia*, but in the former hatching and the first molt occur almost simultaneously.